

THE SOIL FAUNA OF TROPICAL SAVANNAS. II. THE EARTHWORMS

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DISTRIBUTION

There are five large families of earthworms in the world, the Moniligastridae, Megascolecidae, Eudrilidae, Glossoscolecidae and Lumbricidae (Jamieson, 1971), but only four of them are represented in the tropics. The six genera of Moniligastridae are restricted to tropical Asia and eastern Africa; the four subfamilies and 124 genera of Megascolecidae are spread all over the tropics in the eastern and western hemispheres; the 44 genera of Eudrilidae are found in tropical Africa, and the 56 genera of Glossoscolecidae live in the Neotropics (Edwards and Lofty, 1972; Reynolds and Cook, 1976). The four sub-families and 26 genera of Lumbricidae are basically Palearctic in distribution and are mostly limited to temperate and cold latitudes. They are sometimes found in warm temperate climates, such as those of the extreme south of Africa, Australia and New Zealand, though never entering tropical savannas (Lee, 1959; Reinecke and Ljungström, 1969).

The structure and morphology of the four tropical families of earthworms closely resemble those of the most primitive Oligochaeta. Except in the Moniligastridae and some Eudrilidae, the gizzard and the clitellum are located in the anterior part of the animal (segments 5–6 for the gizzard and 13–20 for the clitellum). These organs are placed much further back in Lumbricidae, which allows for the development of a strong musculature, very seldom found in tropical earthworms (Bouché, 1972).

ECOLOGICAL CATEGORIES

The obvious relationships existing between structure and life history of earthworms have led many

authors to individualize a number of life-forms (Franz, 1950; Lee, 1959; Bouché, 1971, 1977). Among the Lumbricidae, Bouché thus recognized the following three major ecological categories:

(1) The litter-dwelling or **epigeic** earthworms live in the soil litter or other media rich in organic matter such as dung, or under bark. They are of small size and very active, coloured red in forest or formerly forested habitats and green in grasslands. Their burrowing musculature is reduced and they spend the harsh period(s) of the year as cocoons. Their life-span is short, their energy metabolism high and their population turnover rapid.

(2) The soil-dwelling or **hypogeic** earthworms live within the soil and feed upon its humic substances or sometimes on dead roots. Their size is moderate to large and they are not pigmented. Their burrowing musculature is well developed, and they can withstand unfavourable environmental conditions by becoming inactive, resuming an active life as soon as temperature and/or soil moisture again reach suitable levels. Their energy metabolism is low, and population turnover is slow.

(3) The **aneic** earthworms are for the most part large-sized animals which spend most of their lifetime within the soil, occasionally coming to its surface to feed on litter material. Their colour is usually dark brown, pigmentation being often limited to the dorsal, if not anterodorsal, part of the body in species which usually leave their terminal segments in their burrow. The burrowing musculature is well developed, and these earthworms become inactive when adverse conditions prevail. Their population dynamics appear to be variable from one species to another.

Hence, the adaptive strategies of the three above defined life-forms are very different. Litter-dwelling

earthworms offset the heavy mortality rate due to the instability and insecurity of their environment by a high fecundity and a rapid growth rate, in turn made possible by an energy-rich food, the litter. On the other hand, the soil-dwelling earthworms being less exposed in their rather stable soil environment, can offset the disadvantage of a reduced fecundity and slow growth rate resulting from an energy-poor diet. Anecic earthworms combine the advantages of both categories.

These life-forms were defined by Bouché (1971) for Palaearctic lumbricids, but they apply to other families as well. However, true anecic earthworms have not yet been found in tropical habitats (Lavelle, 1978; Lavelle et al., 1981). The presence of a gizzard in the anterior part of the animal has apparently made the development of a strong musculature impossible. On the other hand, the soil-dwelling and soil-eating (*geophagous*) earthworms are very numerous in the tropics, and three ecological sub-categories can be distinguished — oligohumic, mesohumic, and polyhumic — depending upon the amount of humic substances present in their preferred habitat.

Oligohumic earthworms live in soils very poor in organic matter — that is, in the deeper portion of the soil profile. **Mesohumic** species are found between the soil surface and a depth of about 20 cm, where the soil is moderately rich in organic substances. On the other hand, **polyhumic** earthworms feed upon pockets of soil enriched with organic debris, such as small decomposing roots, or in the thin surface layer rich in organic matter; their small size may also lead them to ingest the smallest soil particles which are most often also the most energy-rich.

PROXIMATE AND ULTIMATE FACTORS INFLUENCING THE ACTIVITY AND DISTRIBUTION OF SAVANNA EARTHWORMS

A number of environmental parameters, both physical and biotic, play a key role in the activity cycle and distribution of tropical earthworms and help one to understand their community structure.

Soil moisture

This is quite certainly the most important of all environmental variables for earthworms in tropical

soils. It obviously depends first of all on the amount of rainfall and its pattern of seasonal distribution. But other factors also have to be taken into consideration, among them the physical characteristics of the soil (its water-holding capacity), the local topography, the nature and density of the vegetation cover, and the regular occurrence of grass fires (Clément, 1980). As shown in Fig. 22.1, the water content of a savanna soil not only varies continuously throughout the year, but is very different in the various facies of the same savanna landscape. At Lamto (Ivory Coast), the soil of the study plot, located in a shallow depression in grass-derived savanna, is more humid than that of the shrub savanna plot on the plateau. The driest soils of the Lamto area are those of the gallery forests, since the evaporation rate is the highest there. Generally speaking, grass savanna soils are more humid than those of the shrub and tree savannas for the same reason (Lavelle, 1978).

As a consequence of their cutaneous respiration, earthworms are extremely sensitive to drought. As soon as soil moisture reaches a given threshold, usually a little above the wilting point for plants (pF 4.2), earthworms empty their gut, coil up inside a little earth cavity plastered with mucus, and become inactive (Lavelle, 1971a). If the rains are delayed for too long, most of them will die, but their cocoons are usually far more resistant to drought than adult individuals, and will ensure the future of the population. The duration of the dry season is therefore of prime importance in determining earthworm distribution; they cannot live in the driest (Sahelian) savannas. Soil moisture also influences the activity of earthworms, as shown in Fig. 22.2.

Soil temperature

It is well established that under natural conditions the soil temperature of tropical savannas remains remarkably stable throughout the year. However, when any disturbance takes place which destroys most of the plant cover, whether it be by burning or mowing, the temperature conditions are totally changed and the upper layers of the soil can become hotter than the surrounding atmosphere. For instance, a few days after burning, when a thick layer of black ashes still remained on the ground, Athias (1974) recorded a temperature exceeding

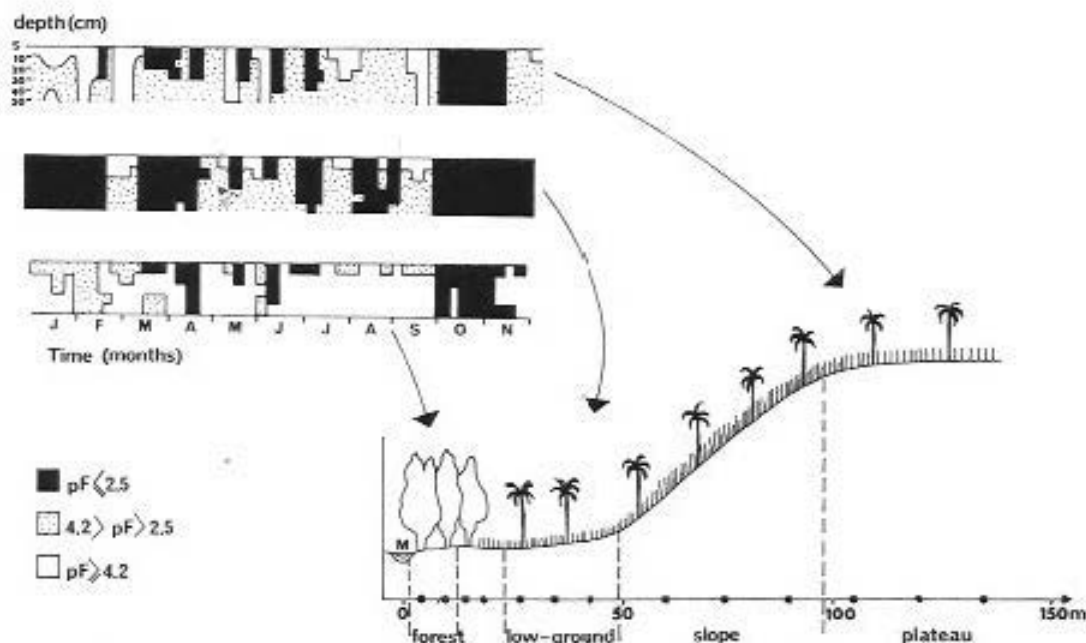


Fig. 22.1. Water regime of soils at different topographic levels in the same savanna landscape (Lamto, Ivory Coast, 1969; after Lavelle, 1978).

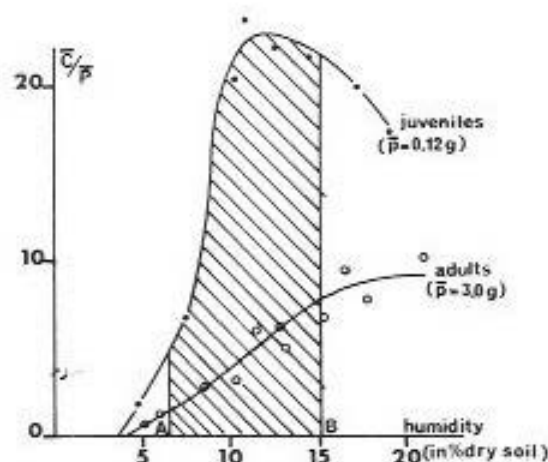


Fig. 22.2. Variations in the soil consumption (C/P) of *Millsonia anomala* (Megascolecidae) as a function of soil moisture, all other factors being equal (A and B are the limits of monthly mean values of soil moisture observed in the field and \bar{p} is the average weight of the two age categories of worms) (after Lavelle et al., 1974).

50°C in the uppermost few centimetres of the soil at Lamto.

Soil temperature definitely influences the activity

of earthworms. Even slight thermal variations can change the rate of ingestion of earth by *Millsonia anomala*, a geophagous species; this is particularly true in younger individuals (Fig. 22.3). The surface activity of these same earthworms is also affected by soil temperature. When soil surface temperature increases, earthworms have to move into the deeper parts of the soil, where nutrients exist in smaller quantities (Fig. 22.4).

Other factors

The granulometric and mineral composition of the soil can also modify earthworm distribution, mostly through their influence on soil water-holding capacity. The same applies to the plant cover, but only in part, as the level of earthworm populations will depend upon the amount of litter and roots produced by the vegetation. Once dead, this plant material will be consumed by the worms immediately, or after transformation by micro-organisms. The amount and nutritional quality of the food thus made available deeply influences the growth rate of young earthworms, as exemplified by the sharp differences in growth rate of young

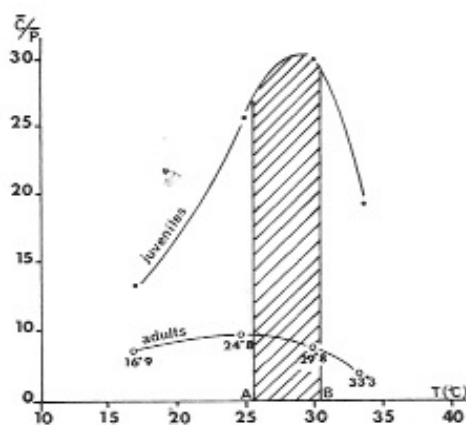


Fig. 22.3. Variations in the soil consumption (C/P) of *Millsonia anomala* as a function of soil temperature, all other factors being equal (A and B: see Fig. 22.2) (after Lavelle, 1975).

Millsonia anomala raised in earth samples taken at different depths in the soil (Fig. 22.5).

Among biotic factors, the influence of predation and parasitism is hard to estimate in field conditions. Bird predation on tropical earthworms seldom occurs in tropical savannas, as a result of the thickness of the grass cover and the subterranean habits of most of the worms. Other predators do exist, however: doryline ants, mole crickets, shrews and mongooses, not to mention predatory earthworms of the genus *Agastrodilus*. Some parasites are also known, including small ectoparasitic Enchytreidae. Nevertheless, predation pressure is probably quite small. Senapati (1980) found fungal infections in senescent and dead *Octochaetona surensis*.

NUMBERS AND BIOMASS OF SAVANNA EARTHWORMS

The available data are tabulated in Table 22.1. However, it is difficult to compare the figures obtained, as both the extraction methods and the areas sampled are not the same. The formaldehyde technique widely used in temperate habitats gives fairly satisfactory results as long as the worms are not aestivating (Lakhani and Satchell, 1970; Bouché, 1969). However, this method is far less suitable for tropical earthworms which, unlike

anecic lumbricids, do not live in extensive burrow systems with surface apertures. The efficiency of the method then becomes very low, which explains the values obtained by Block and Banage (1968) in Uganda grasslands, and Madge (1969) in Nigerian forests. Reinecke and Ljungström (1969), as well as Lavelle (1971a), have found this technique totally unreliable in other African savannas.

Hand sorting, sometimes combined with flotation, is therefore used by most authors. The method has the advantage that it can be adapted to extract earthworm cocoons and thus enables all stages of the populations to be estimated, but it is unfortunately very time-consuming. I have therefore resorted to a compromise, using hand sorting to collect earthworms in large samples, and flotation on small sub-samples to work out correction factors (Lavelle, 1978).

The size of the samples is also quite different in the various study sites mentioned in Table 22.1, ranging from 1.4 to 288 m². The depth of soil sampled (from 20 to 60 cm below soil surface) is also variable, as well as the duration of the studies (from 2 to 24 months). Comparisons must therefore be made with caution.

The average annual rainfall on all the sites studied exceeded 1000 mm. Three of them, Lamto and Foro Foro in Ivory Coast and Kabanyolo in Uganda, can be considered as undisturbed savannas.

At Lamto, the average annual rainfall is 1275 mm; the dry season is limited to two months, and is not very severe as showers occur from time to time. On the average, the numbers of earthworms range from 91 to 400 m⁻², depending upon both the year and the savanna *facies* considered. The corresponding biomass figures (wet weight) range from 134 to 544 kg ha⁻¹. The average values for the five *facies* studied and the four years concerned are 215 ind. m⁻² and 325 kg ha⁻¹.

At Foro Foro, a tree savanna 250 km further north, the rainfall still reaches 1150 mm, but the dry season lasts longer and is harsher than that of Lamto. During the 1978 rains, the number of earthworms ranged from 460 to 582 ind. m⁻², and the wet biomass from 170 to 223 kg ha⁻¹.

The Kabanyolo "bush" near Kampala has an average rainfall of 1500 mm, but the formaldehyde technique allowed only 13 ind. m⁻² to be extracted, representing a wet biomass of only 8.4 kg ha⁻¹.

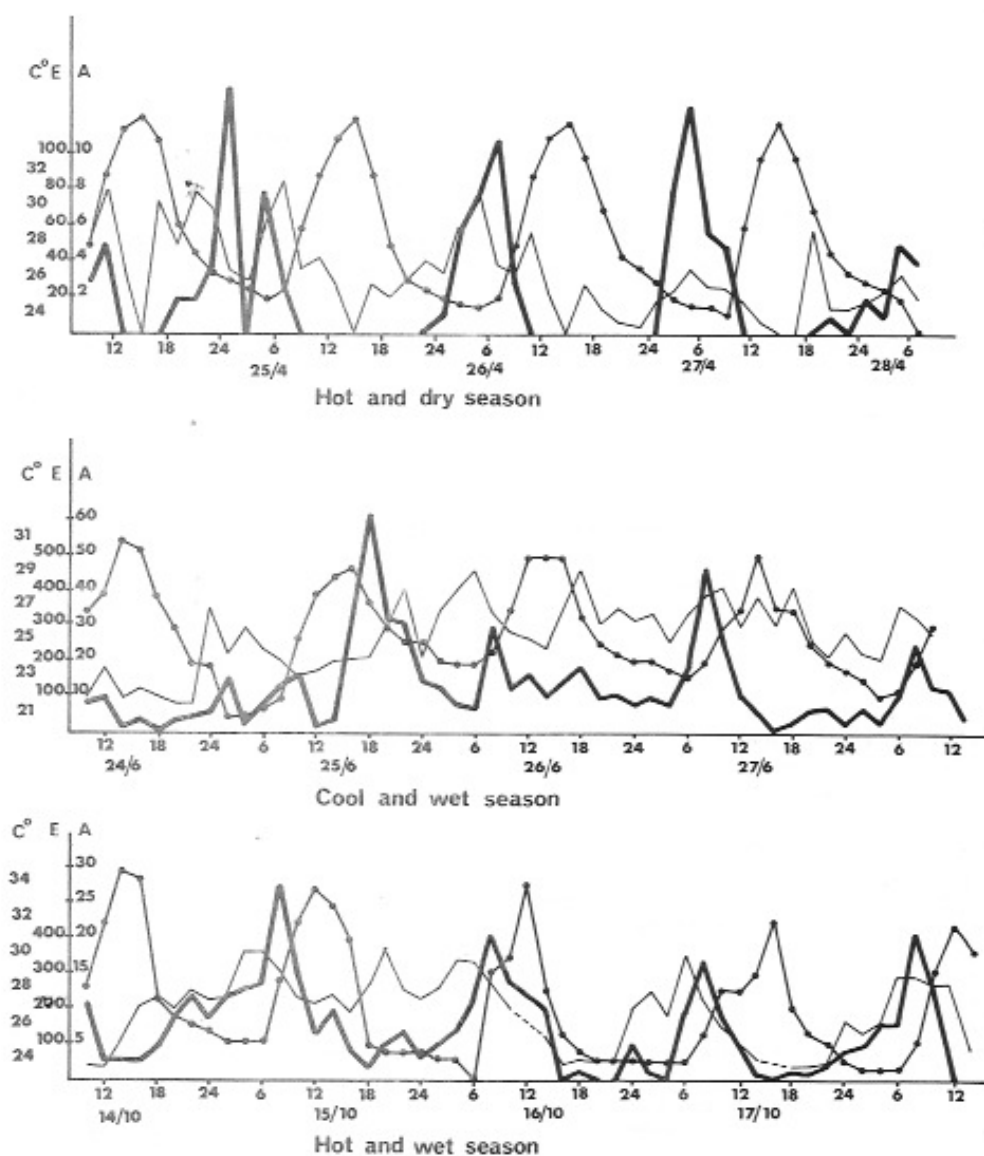


Fig. 22.4. Seasonal variations in the circadian production of surface casts by *Milsonia anomala* (A, heavy line) and eudrilids (E, normal line) on a 10-m² quadrat at Lamto. Air temperature (line with dots) in C°. (After Lavelle, 1978).

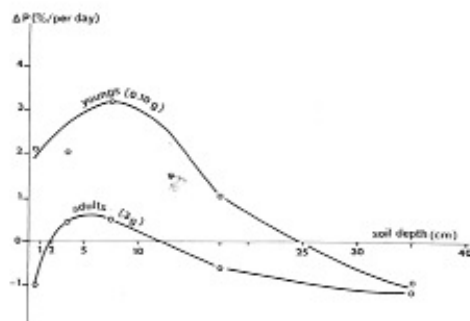


Fig. 22.5. Daily growth increment of *Millsonia anomala*, for young and adult individuals, in soils taken at different depths in the Lamto savanna (pF 2.5; \bar{t} 25.6°C) (after Sow, 1979).

The four other sites are artificial pastures established in formerly forested areas. The highest earthworm densities were found in the Laguna Verde hill pastures (Vera Cruz, Mexico), where the annual rainfall averages 1800 mm. During the rainy season, densities approximate 1000 ind. m^{-2} , the wet biomass reaching 492 kg ha^{-1} (Lavelle et al., 1981). At a lower altitude, between 350 and 50 m above sea level, similar figures were obtained: 600 to 800 ind. m^{-2} and 358 to 555 kg ha^{-1} .

The Indian grassland studied by Dash and Patra (1977) was much poorer in earthworms: 64 to 800 ind. m^{-2} depending upon the season, with an average fresh biomass of 302 kg ha^{-1} . At Sambalpur, the mean annual earthworm densities ranged from 174 ind. m^{-2} in the grazed pasture to 247 ind. m^{-2} in the ungrazed plot. Biomasses were among the highest known so far: 410 kg ha^{-1} in the grazed pasture and 560 kg ha^{-1} in the ungrazed plot. The figures obtained by Breymeyer (1978) in a humid Panama grassland are much lower. This is probably due to the small size of her total sampling area (1.4 m^2) and to the shallowness of her soil samples (20 cm).

If data from the Uganda and Panama sites, where the methods used were inadequate, are excluded there is a steady increase in numbers and biomasses of earthworms with increasing rainfall (Fig. 22.6). The highest values are reached in a grassland grown in former rain-forest areas. It must nevertheless be noted that such figures are much smaller than those recorded in temperate grasslands (560 to 2870 kg ha^{-1} ; Edwards and Lofty,

1972; Nowak, 1975), being closer to those found in temperate forests (370 to 680 kg ha^{-1} ; same sources).

On the other hand, earthworms are more abundant in tropical savannas than in nearby tropical forests. No more than 130 ind. m^{-2} (98 kg ha^{-1}) were found in relict patches of rain forests in the Laguna Verde area, and 75 ind. m^{-2} (34 kg ha^{-1}) in the Lamto gallery forests. This is quite likely due to the relative dehydration of the forest soils at Lamto. During 1969, a dry year in this part of Ivory Coast (annual rainfall 960 mm), the soil moisture remained below the wilting point for plants (pF 4.2) for 25 to 90 days in the various savanna facies, as against 217 days in the gallery forest. This might help to explain why an increase in earthworm number and biomass can sometimes follow deforestation, as at Laguna Verde. This can last as long as the soil has not lost all of its nutrients, as could have been the case in Breymeyer's Panama savanna, if her findings are confirmed by a more satisfactory sampling procedure. It is also possible that all forest earthworms are not equally able to withstand such a drastic environmental change.

COMMUNITY STRUCTURE: RESOURCE PARTITIONING

Knowledge of the community structure of savanna earthworms is at present limited to five sites, two in Ivory Coast (Lamto and Foro Foro), one in Mexico (Laguna Verde), and two in India (Berhampur and Sambalpur).

Lamto

The Lamto earthworm community has the largest number of member species: four Eudrilidae and eleven Megascolecidae (Table 22.2). These fifteen species belong to three different trophic categories: arboreal detritivores (four species), litter detritivores (two species), and soil eaters (geophagous worms) (six species). The three remaining species have specialized diets: one, *Dichogaster* sp. is a termite commensal only found at the bottom of *Trinervitermes* mounds. The two others, *Agastrodilus multivesiculatus* and *A. opisthogynus*, are quite probably predators of other earthworms, at least in part.

TABLE 22.1
Numbers and biomass of earthworms in various savanna study sites

Locality	Savanna category	Rainfall (mm)	Duration of study (months)	Surface sampled (m ²) ¹	Depth (cm)	Extraction method ²	Numbers (ind. m ⁻²)	Biomass (g wet wt. m ⁻²)	Reference
Panama	artificial pasture	1900	3	1.4	20	HS	12-15	0.15-0.36	Beggsmeier (1978)
Laguna Verde, Vera Cruz (Mexico)	hill pasture (800 m)	1800	2	5+0.28	40	HS,W	948	49.2	Lavelle et al. (1981)
	lowland pastures (50-350 m)	1500	2	10+0.28	40	HS,W	620-787	35.8-55.5	
Kabanyolo (Uganda)	"bush"	1500	2	10.7	?	F	13	0.84	Block and Banage (1968)
Berhampur, Orissa (India)	<i>Cynodon dactylon</i> and <i>Hyparrhenia</i> sp. grasslands	1250	18	11.3	20	HS	64-800	30.2	Dash and Patra (1977)
Sambalpur, Orissa (India)	grazed irrigated pasture	1343	13	4.1	40	W	17.4	41.0	Senapati (1980)
	ungrazed irrigated pasture	1343	19	5.9	40	W	24.7	56.0	Senapati (1980)
Lamto (Ivory Coast)	grass savanna	1183	24	288+23.04	60	HS,W	188	38.0	Lavelle (1978)
	shrub savanna	1183	24	288+23.04	60	HS,W	287	48.6	Lavelle (1978)
	unburnt shrub savanna	1276	12	288+23.04	60	HS,W	400	35.9	Lavelle (1978)
Foro Foro (Ivory Coast)	shrub savanna	1150	2	20	60	HS,W	460-582	17.0-22.3	Lavelle (unpubl.)

¹When two different extraction methods have been used on two different soil samples, two figures are indicated.

²Hand-sorting (HS), formalin (F) or soil-washing (W) techniques.

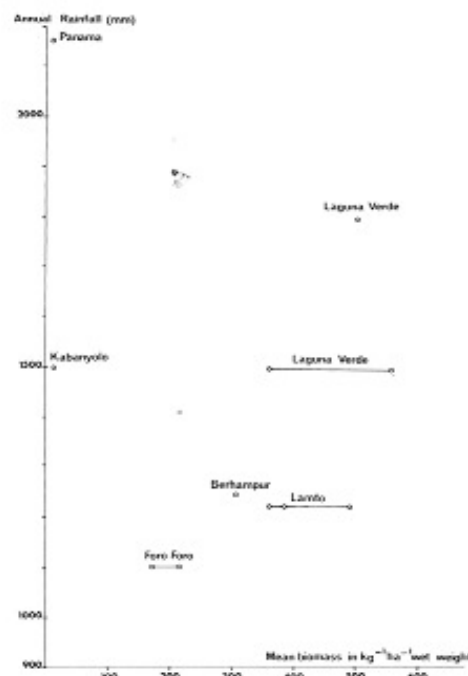


Fig. 22.6. Relationship between earthworm biomass and average annual rainfall in various tropical savanna study sites.

All arboreal detritivores live in "hanging soils"; they are forest species which have found micro-climatic and dietary conditions reminiscent of their original habitat in the small pockets of soil existing between the leaf bases of savanna palms. *Dichogaster bolani* and *D. saliens* are pantropical in their distribution. *D. saliens* and *Chuniodrilus vuattouxi* can also be found at ground level, in rotten tree stumps. *Dichogaster baeri*, a forest species, can also marginally enter the savanna, in the shallow depressions close to gallery forests, and also in grasslands protected from burning for at least fifteen years — that is, already invaded by bush. All these worms are small and dark coloured, *Chuniodrilus vuattouxi* excepted. *Dichogaster baeri* is the only large arboreal earthworm, 15 cm long when adult.

The two litter detritivores, *Dichogaster agilis* and *Millsonia lamtoiana*, respectively brown- and green-coloured, live in the upper few centimetres of the soil and feed upon litter material. *Millsonia lamtoiana* is a large worm which comes out in the

open by night, and also sometimes during the day after heavy rains, or at any time during the mating season; it feeds on large plant debris already partly decomposed and mixed with some soil. *Dichogaster agilis* is smaller, and remains at the soil litter interface, feeding on a mixture of soil and already decomposed plant material. Therefore, these two detritivores are not typical epigeic worms according to Bouché's criteria, being able to dig into the soil and ingest earth with the litter debris they feed on.

All the five remaining species are unpigmented soil-eating (geophagous) earthworms, very seldom found at the soil surface. Some live in the topsoil and produce surface casts. *Millsonia anomala* is the most numerous species in this trophic group; a mesohumic worm, it can reach a body length of 17 cm when adult.

The Eudrilidae are polyhumic worms which live at an average depth of 18 cm, though responsible for numerous casts. Being of small size they feed only on small and energy-rich soil particles, and on tiny organic debris such as decomposing rootlets, or the thin organic layer of the topsoil. The organic matter content of their casts is therefore higher than those of *Millsonia anomala* (Table 22.3).

Dichogaster terrae-nigrae and *Millsonia ghanensis* are both large oligohumic species reaching an adult body length of 70 and 30 cm respectively. They live in the deeper layers of the soil, where the organic matter content is the lowest.

The niches of the different members of the earthworm community are therefore well defined (Lavelle et al., 1980). Spatio-temporal overlap between niches has been estimated using the O_{ij} index (Pianka, 1974). The calculated values for each of the three variables selected (horizontal distribution, vertical distribution, and seasonal cycle of population density) are tabulated in Table 22.4. As the overlap ratios are high for seasonal cycles (0.82 to 0.95, with an average ratio of 0.90), niche separation is mostly achieved through occupation of different savanna facies (index ranging from 0.13 to 0.96; average 0.70) and preference for different soil layers (index ranging from 0.02 to 0.93; average 0.47).

The three variables considered being apparently independent, a resultant matrix can be established by multiplying the calculated values for every species. The results are shown in Table 22.5: the index ranges from 0.01 to 0.80, with an average

TABLE 22.2

Some characteristics of the Lamto savanna earthworms

Species	Family	Habitat	Vertical distribution (cm), range and average depth	Food habits	Maximum wet weight (g)
<i>Chamodrilus vuattouxi</i>	Eudrilidae	"hanging soils" in palm trees	0 to +1800	detritivore	0.08
<i>Dichogaster saliens</i>	Megascolecidae	"hanging soils" in palm trees	0 to +1800	detritivore	0.15
<i>Dichogaster bolani</i>	Megascolecidae	"hanging soils" in palm trees	0 to +1800	detritivore	0.18
<i>Dichogaster bueri</i>	Megascolecidae	"hanging soils" in palm trees	0 to +1800	detritivore	2.50
<i>Dichogaster agilis</i>	Megascolecidae	savanna soil	0 to -30(6)	detritivore	0.60
<i>Millsonia lamtoiana</i>	Megascolecidae	savanna soil	0 to -20(7)	detritivore	22.00
<i>Millsonia anomala</i>	Megascolecidae	savanna soil	0 to -50(8)	mesohumic soil eater	6.00
<i>Chamodrilus zielae</i>	Eudrilidae	savanna soil	0 to -60(18)	polyhumic soil eater	0.20
<i>Chamodrilus palustris</i>	Eudrilidae	savanna soil	0 to -60(18)	polyhumic soil eater	0.20
<i>Stuhlmannia porifera</i>	Eudrilidae	savanna soil	0 to -60(18)	polyhumic soil eater	0.25
<i>Dichogaster terrae-nigrae</i>	Megascolecidae	savanna soil	0 to -60(23)	oligohumic soil eater	28.00
<i>Millsonia ghanensis</i>	Megascolecidae	savanna soil	0 to -60(32)	oligohumic soil eater	16.00
<i>Agastrodrilus opisthogynus</i>	Megascolecidae	savanna soil	0 to -60(29)	oligohumic soil eater and possibly carnivorous	3.50
<i>Agastrodrilus multivesiculatus</i>	Megascolecidae	savanna soil	0 to -60(29)	oligohumic soil eater and possibly carnivorous	4.50
<i>Dichogaster</i> sp.	Megascolecidae	base of termite mounds	?	polyhumic soil eater?	2.00

value of 0.35. Thus spatio-temporal niche separation is quite satisfactory, except for the following two groups of species.

(1) *Dichogaster agilis*, *Millsonia anomala* and *M. lamtoiana*, which live in the topsoil of, preferably, shrub savannas — whether annually burnt or not. In this case, niche separation is achieved by food partitioning: *Millsonia anomala* is a soil eater, whereas the other two species are detritus-feeders. The large *M. lamtoiana* feeds on almost intact litter material, and the small *Dichogaster agilis* eats tiny plant debris already decomposed.

(2) With regard to the second group of worms (*Agastrodrilus opisthogynus*, *Millsonia ghanensis* and the Eudrilidae), the species concerned are of

different sizes and diets: *Millsonia ghanensis* lives in the deeper, energy-poor soil layers, while the Eudrilidae feed on energy-rich soil, and *Agastrodrilus opisthogynus* appears to be partially carnivorous.

Other earthworm communities

Only five species are found at Foro Foro: *Dichogaster agilis* and *Millsonia lamtoiana*, both detritivores; *Stuhlmannia porifera*, a polyhumic geophagous eudrilid; *Agastrodrilus dominicae* which is very close to *A. opisthogynus* in morphology and habits; and *Dichogaster terrae-nigrae*, a large soil eater which is represented here by a small-sized

TABLE 22.3

Granulometric composition and organic matter content of casts from Eudrilidae and *Millsonia anomala* in a grass savanna of Lamto (Ivory Coast)

	Eudrilidae	<i>Millsonia anomala</i>	Control soil (0 to -40 cm)
Clay (<2 µm)	5.0	5.2	3.3-3.7
Fine silt (2-20 µm)	7.3	8.6	5.7-6.5
Coarse silt (20-50 µm)	12.0	11.5	7.5-8.5
Fine sand (50-200 µm)	40.0	27.0	25.5-29.0
Coarse sand (200-2000 µm)	32.0	46.5	50.5-56.5
C(%)	10.1	5.8	1.9-8.2
N(%)	0.76	0.57	0.17-0.57
C/N	13.3	10.2	10.8-15.3
Organic matter (%)	1.7	1.0	0.6-1.4

form, living closer to the soil surface (16 cm on the average, instead of 28 cm at Lamto).

In the Laguna Verde grasslands, only three species are found: *Diplocardia koebeli*, a polyhumic soil eater of small size (maximum wet weight: 0.30 g); *Ponchoscolex corethrurus*, a mesohumic geophagous species reaching a body weight of 1 g when adult; and *Dichogaster* sp., a small detritivore weighing no more than 0.40 g (Lavelle et al., 1979b).

The Indian pastures of Sambalpur harbour five species whose diets remain unknown. Adult weights range from 0.09 g (*Ocnerodrilus occidentalis*) to 1.22 g (*Lampito mauritii*), the three other species (*Drawidia willsi*, *D. calabi*, *Octochaetona surensis*) weighing 0.13 g, 0.54 g and 1.08 g, respectively.

The Berhampur community is composed of only two species: a detritivore *Lampito mauritii* (maximum body weight 0.60 g) and a small soil-eating member of the Ocnerodrilidae (M.C. Dash, pers. comm., 1979).

Comparisons

Although the number of communities studied is very small, a few tentative conclusions can be reached.

First, soil-eating (geophagous) worms are the most numerous in the four savanna communities studied. This is quite probably due to the suitable

and well-buffered microclimatic conditions in tropical savanna soils, as well as to the large amount of organic matter provided, at all soil depths, by the rapid decomposition of litter and roots. The amount of nutrients thus made available to soil organisms is also increased by the lack of detritivorous earthworms, ascribable to the sharp seasonal changes in environmental conditions at the soil/litter interface.

Second, under similar climatic conditions, species richness is much greater in "natural" savannas than in man-made and man-maintained pastures.

Third, even in the more species-rich savannas, niche overlap is apparently very limited: size differences, time and space partitioning, as well as food partitioning, all contribute to reduce, if not avoid, interspecific competition.

Fourth, the adult size of a species seems to be closely related to the duration of the dry season. The populations of large species are apparently more sensitive to drought than those of small species. At Lamto, where the dry season is restricted to one or two months per year, most earthworms are of a large size, and their adult weight exceeds 1 g, even reaching 20 to 30 g for the largest species. At Sambalpur, where the annual rainfall is very similar to that of Lamto, but where the dry season extends over six months, only small earthworms are found, the largest adult individuals not exceeding 1.5 g in weight.

SEASONAL VARIATIONS IN ACTIVITY AND NUMBERS

A marked seasonality of environmental conditions is one of the major characteristics of tropical savannas. During the dry season the soil moisture often drops to give a pF of 4.2 and even 4.7 at Lamto. Earthworms then become inactive, the inactivity threshold ranging from pF 4.2 to 3.0 according to the species (Lavelle, 1971a). However, the water content of the soil also varies with depth, and this explains why the seasonal cycles of different species can differ to a certain extent.

Activity cycles

In the derived savanna at Lamto a proportion of earthworms, variable according to the species concerned, become inactive from December to March (the "long" dry season). Then comes the rainy season during which worms are all very active before entering a second period of inactivity in August and September, during the "short" dry season. Activity levels are high again in October and November.

However, there are marked differences between the activity cycles of worms living in the various kinds of savanna, as shown in Fig. 22.7. In 1972, an average year at Lamto (yearly rainfall 1276 mm), the number of months per year during which over 50% of the earthworm population remained inactive ranged from three in old unburnt savannas with strong bush encroachment, and two in shrub savannas, to none in grass savannas. In the same savanna categories, the periods during which 10 to 50% of the worm population remained inactive were respectively of four, four and five months.

Seasonal changes in numbers and biomass

Obviously there are some relationships between seasonal variations in earthworm activity and their changes in number. The fact that every species has its own pattern of seasonal variation in numbers (Fig. 22.8) implies that environmental variables do not have the same importance for all sympatric species. Indeed, this can be established by calculating the relationship between population density and each of the eight environmental factors previously identified by multivariate analysis (Table 22.6).

Thus, population numbers of *Millsonia lamtoiana* and *Dichogaster agilis*, both detritivores, and of the polyhumic soil-eating Eudrilidae are negatively correlated with a factor corresponding to the trophic effects of grass fires. This factor alone accounts for 26 to 56% of the seasonal variance of their numbers. On the other hand, *Millsonia ghanensis* and *Agastrodrilus* spp., which live in the deeper soil layers, are affected very little by environmental factors; these are responsible for only 21 to 23% of the variance of their numbers.

In between these two species groups, the numbers of *Millsonia anomala*, a mesohumic earth feeder, and of *Dichogaster terrae-nigrae*, an oligohumic earth feeder, are influenced by other environmental factors. The abundance of the first species depends on the water regime of the soil related to the presence of a shrub cover; that of the second species is mostly influenced by drainage conditions of the soil (Lavelle, 1978).

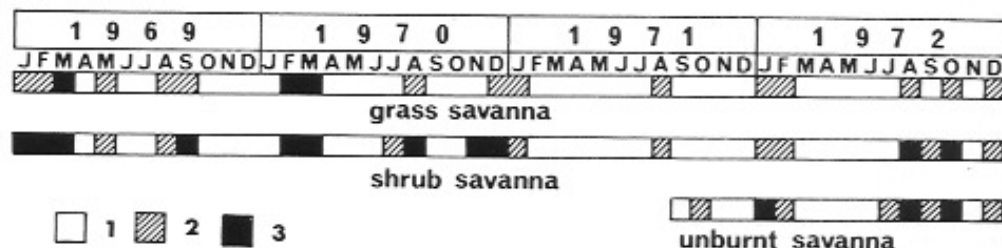


Fig. 22.7. Seasonal variations in earthworm activity in different savanna types at Lamto (after Lavelle, 1978). 1: all worms active; 2: 0 to 50% of quiescent individuals; 3: 50 to 100% of quiescent individuals.

TABLE 22.4

Spatio-temporal niche overlap (O_{st} index) in the earthworm community of Lamto savanna (Ivory Coast)

A. For vertical distribution

M.l.	0.93						
M.a.	0.91	0.96					
D.t.	0.11	0.44	0.49				
Eu.	0.38	0.48	0.62	0.57			
A.o.	0.08	0.10	0.27	0.33	0.91		
M.g.	0.02	0.05	0.24	0.29	0.77	0.88	
	D.a.	M.l.	M.a.	D.t.	Eu.	A.o.	

B. For horizontal distribution

M.l.	0.95						
M.a.	0.73	0.89					
D.t.	0.13	0.55	0.74				
C.z.	0.94	0.53	0.79	0.75			
S.p.	0.54	0.95	0.82	0.47	0.41		
A.o.	0.76	0.56	0.97	0.71	0.72	0.92	
M.g.	0.64	0.37	0.89	0.55	0.53	0.95	0.96
	D.a.	M.l.	M.a.	D.t.	C.z.	S.p.	A.o.

C. For seasonal cycle

M.l.	0.80						
M.a.	0.94	0.91					
D.t.	0.84	0.92	0.95				
Eu.	0.93	0.87	0.93	0.94			
A.o.	0.82	0.91	0.92	0.99	0.95		
M.g.	0.80	0.89	0.91	0.94	0.87	0.95	
	D.a.	M.l.	M.a.	D.t.	Eu.	A.o.	

Legend: D.a. = *Dichogaster agilis*; M.l. = *Millsonia lamtoiana*; M.a. = *Millsonia anomala*; D.t. = *D. terrae-nigræ*; Eu. = *Eudrilidae*; C.z. = *Chuniodrilus zielæ*; S.p. = *Stuhlmannia porifera*; A.o. = *Agastrodrilus opisthogymus*; M.g. = *M. ghanensis*.

TABLE 22.5

Total niche overlap in the earthworm community of the Lamto savanna; same symbols as in Table 22.4

M.l.	0.71						
M.a.	0.62	0.65					
D.t.	0.01	0.21	0.34				
C.z.	0.33	0.40	0.46	0.40			
S.p.	0.19	0.11	0.47	0.25	0.41		
A.o.	0.04	0.05	0.24	0.23	0.62	0.79	
M.g.	0.01	0.02	0.18	0.15	0.36	0.64	0.80
	D.a.	M.l.	M.a.	D.t.	C.z.	S.p.	A.o.

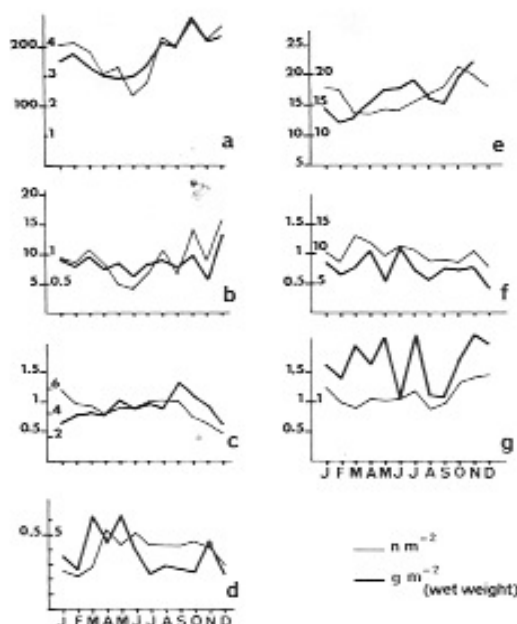


Fig. 22.8. Average seasonal changes in numbers and biomass of Lamto earthworms: a, Eudrilidae; b, *Dichogaster agilis*; c, *Millsonia ghanensis*; d, *M. lamtoiana*; e, *M. anomala*; f, *D. terraenigrae*; g, *Agastrodrius opisthogynus* (after Lavelle, 1978).

Seasonal variations of the functional structure of the populations

Seasonal variations in activity and numbers also go together with changes in the functional structure defined by the weight distribution of the worms, the percentage of inactive individuals, the vertical distribution of populations in the soil and the production of cocoons. Therefore, stages of population decrease, increase and *status quo* alternate during the year, but in different ways (Fig. 22.9).

Lavelle and Meyer (1976) and Lavelle (1978) have made use of a technique of multivariate analysis of mixed data to identify seven different population stages in the Lamto earthworm community. Each of these stages differs from the others by the number and biomass of worms (axis I), the percentage of active individuals (axis II), and relative distribution in depth of the population (axis III). When monthly samples are taken, the seasonal changes in the structure and function of the populations can be followed throughout the year. All sympatric species are then found not to behave in the same way. In the shrub savanna, for instance, even two congeneric species, *Millsonia anomala* and *M. lamtoiana*, do not display the same patterns of change in functional structure.

TABLE 22.6

Correlations between the density of earthworm populations and the current values of the major environmental factors previously identified by multivariate analysis (Lavelle, 1978); values are given in percentage of the variance explained; the symbols + or - indicate whether the relationship is positive or negative

	Grass fires	Dry and hot spells	Cool spells	Thickness of vegetation cover	Soil drainage	Percentage of the total variance explained (%)
<i>Millsonia lamtoiana</i>	56 -	2 -	3 -	1 -	1 +	63
Eudrilidae	44 -		1 -	5 +	3 +	54
<i>Dichogaster agilis</i>	26 -					26
<i>Millsonia anomala</i>	2 -			17 -	3 +	22
<i>Agastrodrius</i> spp.	2 -	7 -			7 +	15
<i>Millsonia ghanensis</i>	6 +	4 -	3 +		5 -	18
<i>Dichogaster terraenigrae</i>	1 -	5 -		3 +	48 +	58

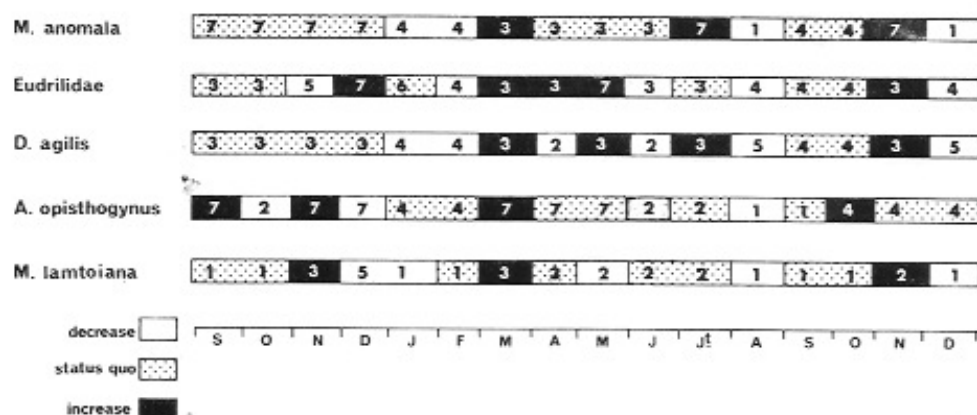


Fig. 22.9. Seasonal changes in the functional structure of some earthworm populations at Lamto, from September 1971 to December 1972. Stages are ranked from 1 to 7. *A* stands for *Agastrodrilus*, *D* for *Dichogaster*, and *M* for *Millsonia*. (After Lavelle, 1978.)

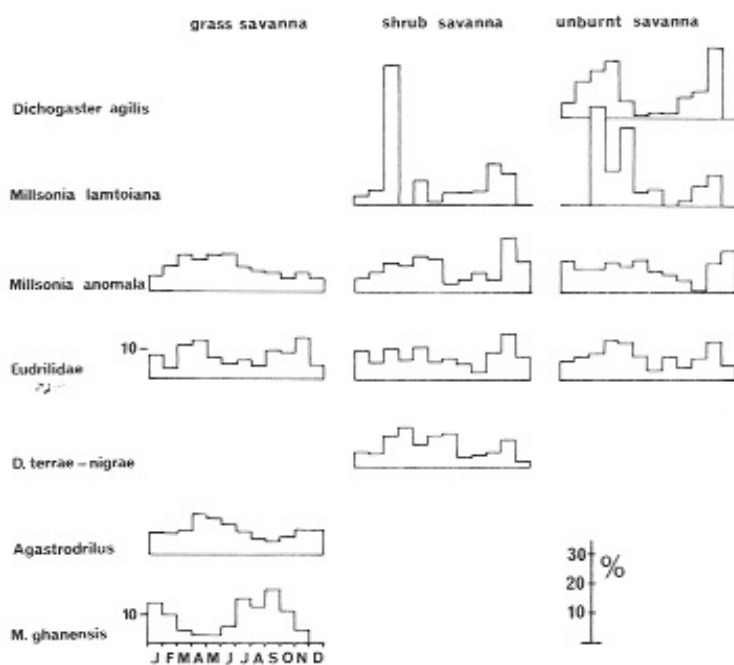


Fig. 22.10. Monthly variations in production of Lamto earthworms in three savanna types in 1972 (after Lavelle, 1978).

Seasonality in production

Seasonality in production, hence the trophic impact of the population, is closely linked to such seasonal changes. In the Lamto savanna, production is highly seasonal among detritivorous species living in the litter, such as *Millsonia lamtoiana* and *Dichogaster agilis*. Seasonality in production is also perceptible, however, even in species living deeper in the soil (Fig. 22.10). On the whole, the highest figures are reached during the rainy season, and the lowest during the dry season, or when there is a temporary excess of rain. This seasonality in production is also much more obvious in shrub savannas than in grass savannas, being closely correlated with the instability of the water regime of the soil in the former.

Seasonality in production is even more accentuated in savannas where the climate is much more seasonal than in Lamto. At Berhampur, for example, *Lampito mauritii* populations are only active for a few months each year (Dash and Patra, 1977).

POPULATION ECOLOGY

Little is known concerning the population structure and dynamics of savanna earthworms; so far, only a few species of the Lamto area have been adequately studied.

Demographic profiles

Demographic profiles can be established on the basis of the following three parameters: the dura-

tion of the growth period (D , in months), the life expectancy of the hatchlings (E_h , in months), and the number of cocoons produced per individual per year (F). It has been shown (Lavelle, 1979a) that these three parameters vary together (Table 22.7). They can be combined in a demographic index:

$$D = 10^3 F/C E_h$$

which is directly related to another index, called the ecological index:

$$E = \log W_s \bar{p}$$

which summarizes the life-style of the species, on the basis of its maximum body weight (W_s) and the average depth at which they are living within the soil (\bar{p}).

In the community studied, population turnover is all the more rapid when species are small, and live close to the soil surface; this is mediated by an accelerated growth, a short life expectancy and a high fecundity. The small size and high metabolic rate of the smaller earthworms allow them to grow quickly when enough food is available, as is the case in the litter. On the other hand, species living close to the soil surface are more exposed to predation and to the disruptive action of periodic grass fires and severe drought spells.

In a community like this, earthworm species can be ranked along an r - K gradient, according to the values of their D index, indicating their ability to increase their numbers, an ability which itself depends on their ecological characteristics assessed by their E index (Fig. 22.11).

TABLE 22.7

Some demographic characteristics of seven of the most numerous populations of Lamto earthworms (Lavelle, 1979)

	Duration of the growth period (in months)	Number of cocoons produced per adult, per year	Expectation of life at hatching (months)	Demographic index	Ecological index
	C	F	E_h	$D = 10^3 F/C E_h$	$\log W_s \bar{p}$
<i>Chuniodrilus zielae</i>	18	13.0	3.3	219	3.2
<i>Dichogaster agilis</i>	15	10.7	3.4	210	3.0
<i>Millsonia anomala</i>	20	6.2	6.2	50	32
<i>Millsonia lamtoiana</i>	24	3.1	7.5	17	210
<i>Dichogaster terraenigrae</i>	36	1.9	11.6	4.5	575
<i>Agastrodrius opisthogymus</i>	24	1.3	11.1	4.9	87
<i>Millsonia ghanensis</i>	42	1.3	10.6	2.9	512

Outside Lamto, there is also some information on the demographic characteristics of two other species, *Lampito mauritii* in India (Dash and Patra, 1977; and pers. comm.) and *Ponchoscolex corethrurus* in Mexico (pers. obs.).

Lampito mauritii lives at an average depth of 12 cm, seldom reaching 20 cm. Its size is small, the maximum adult body weight not exceeding 0.60 to 0.70 g (wet weight). Annual fecundity is probably high, as the population density can change from 16 to 240 ind. m⁻² in three months. Such a rapid increase in numbers implies that every adult produces at least fifteen young per year — that is, seven to 10 cocoons, as each cocoon gives rise to one or two young (M.C. Dash, pers. comm.). The average life expectancy at birth ranges from 3.5 to 4.0 months, and growth is very rapid. Sexual maturity occurs at one year of age. Nevertheless, the worms continue to grow afterward, the maximum body weight being reached between 12 and 15 months of age. The demographic index (*D*) is therefore of the order of 200 to 300, which means that this worm has the ability to build up its numbers very quickly. Its ecological index (*E*) is low, and the species would stay close to *Chuniodrilus zielae* and *Dichogaster agilis* on Fig. 22.11.

Ponchoscolex corethrurus, a mesohumic soil eater, is somewhat larger, reaching a maximum adult weight of 1.0 g. It lives in the topsoil, seldom burrowing deeper than 10 cm below the soil surface (5.9 cm deep on average). The growth is rapid, young worms increasing their body weight by 7.5% daily, during their first five weeks of life. Fecundity is high, at least three to four cocoons being produced per adult during the reproduction period, in field conditions, and five cocoons per adult during six weeks of laboratory rearing.

Similar data are unfortunately lacking for temperate species. However, the tropical savanna earthworms already studied are definitely more prolific than many European lumbricids, whose fecundity is low and growth rate slow.

Demographic strategies

The above-mentioned data have already shown that tropical earthworm species living in a single savanna can easily be ranked along a *r-K* continuum. At Lamto, the oligohumic soil eaters *Dichogaster terrae-nigrae* and *Millsonia ghanensis* are typical *K*-strategists. Both are large species,

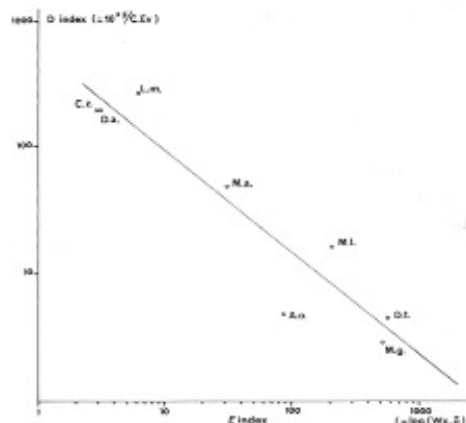


Fig. 22.11. Relationship between the ecological, $E = \log W_s \bar{p}$, and demographic indices, $D = 10^3 F/C \cdot E_s$, for eight species of tropical earthworms (W_s = maximum weight of the species; \bar{p} = average depth at which the earthworm population is found; F = fecundity of adult individuals — that is, number of cocoons produced per year; C = total duration of the growth period; E_s = life expectancy of young at birth). Legend: C.z. = *Chuniodrilus zielae*; D.a. = *Dichogaster agilis*; L.m. = *Lampito mauritii*; M.a. = *Millsonia anomala*; M.l. = *M. lamtoiana*; A.o. = *Agastrodrius opisthogymus*; D.t. = *D. terrae-nigrae*; M.g. = *M. ghanensis*. (After Dash and Patra, 1977; Lavelle, 1979a.)

growing slowly and having a low fecundity; both also live in the deeper soil layers, a rather stable environment, but one poor in organic matter. Their *D* index is less than 5.

Small arboreal detritivores, such as *Dichogaster bolaii* and *D. saliens*, the topsoil detritivore *D. agilis*, and the small polyhumic eudrilids are at the other end of the *r-K* gradient. Their size is small, their growth rate accelerated, and their fecundity high. They live in the energy-rich layers of the soil, but are at the same time more exposed to predators and climatic accidents. Their *D* index values are 200 or more. The Indian species *Lampito mauritii* also belongs to this category of *r*-strategists.

The large detritivore *Millsonia lamtoiana* ($D = 17$) and the smaller mesohumic soil eater *M. anomala* ($D = 50$) are in an intermediate position on the *r-K* continuum. However, *M. anomala* can temporarily adapt its demographic characteristics to adverse conditions; when rainfall is less than usual, its *D* index can reach 107 in shrub savannas.

In drier Sudanian savannas, such as at Foro Foro, the large *K*-strategists disappear first, as well as *Millsonia anomala*. Only *Dichogaster terraenigrae* remains, but it changes its diet and reduces its body length. Further north, the only earthworms left are *r*-strategists, small detritivores and polyhumic soil-eating eudrilids living in the topsoil. Humid grasslands growing in formerly forested areas are also colonized by *r*-strategists, such as the pantropical *Ponchoscolex corethrurus*. No *K*-strategists are found in such marginal habitats.

Population dynamics

Here again, the few data available are those of Lamto, where the population dynamics of a very common species *Millsonia anomala* has been comprehensively studied (Lavelle, 1978; Lavelle and Meyer, 1976, 1977).

Rate of growth. Field observations and laboratory experiments show that four major variables are able to influence the growth rate of *Millsonia anomala*: its body weight (i.e. its age), and the moisture, temperature and organic matter content of the soil.

The rate of growth is more rapid when the worm is young. Then, it decreases rapidly, up to sexual maturity, to diminish more slowly during the remainder of the life-span.

Soil moisture is very important to ensure optimal growth, especially for adult worms which are less resistant to drought than immature ones. The growth of adult *Millsonia anomala* is discontinued when the water content of the soil is lower than 10%, as against 8% for immature individuals. Maximum daily growth increments are reached at a soil moisture content little above 20% for adult, and 13% for young worms (pF 2.5 = 12%; pF 4.2 = 4% in *Sich* soils) (Fig. 22.2).

Soil temperature is also important. Maximum growth increments are obtained at 24.8°C for adult individuals and 29.8°C for young ones; growth stops below 19.0°C and above 35°C, for all ages.

All other factors being equal, it is the organic matter of the soil which is determinant. A larger growth increment is observed in the soil layers where organic matter is the most abundant — that is, in the first 10 cm of soil. However, the quality of organic material consumed is also important; optimal growth rates are reached at depths ranging from 5 to 10 cm, and not closer to the soil surface.

Mortality rate. Correlations between monthly mortality rates of *Millsonia anomala* and a number of population and environmental variables show that two of the environmental parameters exert a major influence on mortality. Dry and hot spells increase it significantly, whereas burning of the grass has the opposite effect. Population density does not play any role in the mortality of this species.

Natality rate. A similar approach has been used to determine the most important variables influencing natality. In this case the most highly correlated variables are not those which operate at the time of hatching, but three months earlier. Spells of dry and hot weather, here again, have an unfavourable effect on population dynamics, diminishing the number of cocoons produced by the adults; overcrowding has similar effects. On the other hand, the thickness of the vegetation cover, whether it be grass or shrubs, has a favourable effect on natality, probably by keeping the soil moist for a longer time.

A simulation model showing the ways by which the different population and environmental variables interact has been proposed by Lavelle and Meyer (1977).

The population dynamics of some other sympatric species of Lamto earthworms is, however, influenced by environmental factors in a way different from that for *Millsonia anomala*. As shown on Table 22.6, *M. lamtoiana*, *Dichogaster agilis* and the eudrilids which live in the litter or the top soil, are more affected by burning and less dependent on the thickness of the vegetation cover than *M. anomala*. In general, earthworm populations with a high turnover appear to be more susceptible to environmental influences than those with a slow turnover; susceptibility to population pressure is also greater in *K*-strategists.

THE EFFECTS OF EARTHWORMS ON SAVANNA SOILS

The mechanical role earthworms play within the soil has been known for a long time, but the details of this action are still very poorly understood, especially in the tropics. First of all, they bury and incorporate plant remains from the litter into the soil, assimilating and mineralizing part of the

organic matter ingested. However, the unassimilated soil is also modified during its passage through the worm's gut, and these modifications have some impact on soil micro-organisms. Furthermore, the production of surface casts by a number of species improves drainage and aeration of the soil itself.

Energy transformation by savanna earthworms

The fate of the energy ingested during the year by a *Millsonia anomala* population in a Lamto grass savanna has been described by Lavelle (1977). Living in soils poor in organic matter (1% on the average), this species ingests huge amounts of soil yearly. For example, every young individual ingests 20 to 36 times its own body weight of dry soil every day, the ratio diminishing as the worm grows older, however. This means that an average *Millsonia anomala* can ingest from 3 to 5 kg of soil per year, and that a natural population of 215 000 ind. ha⁻¹ ingests about 500 tons ha⁻¹ yr⁻¹ (wet weight). It has been estimated that the amount of soil which passes yearly through the entire earthworm community at Lamto approximates 850 to 1200 tons ha⁻¹.

The assimilation efficiency (*A/I* ratio) of soil-eating earthworms is low, from 7 to 10%. Most of the assimilated energy is used for respiration and mucus production, and less than one-tenth for growth and reproduction. Therefore, the ecological growth efficiency (*P/I* ratio) is extremely low, about 0.3%. Similar values are common among soil-eating worms in Lamto (*Dichogaster terrae-nigrae*, 0.9%; *Millsonia ghanensis*, 0.9%), as well as in Europe (*Allobophora rosea*, 0.2 to 0.6%; Bolton and Philippon, 1976). The ecological growth efficiency is, however, slightly better in larger species such as *Millsonia ghanensis* and *Dichogaster terrae-nigrae*, than in smaller ones such as *M. anomala*.

Litter-dwelling earthworms are a little more efficient. Litter consumption by the two Lamto species, *Dichogaster agilis* and *Millsonia lamtoiana* ranges from 180 to 980 kg ha⁻¹ yr⁻¹ depending upon the savanna categories concerned, and their production varies from 25.3 to 216 kg ha⁻¹ yr⁻¹, respectively. The *P/I* ratio is also higher for the larger species (1.8%) than for the smaller one (0.4%).

Soil mixing and its consequences

Most of the energy assimilated by earthworms being used for muscular activity, it is easy to understand why the mechanical role of these animals is so important. In the 1000 t ha⁻¹ of soil which on the average pass every year through the gut of Lamto earthworms, there are about 14.7 tons of organic matter, which correspond to one-third of the humus fraction of this soil (c. 44 t ha⁻¹). Less than 3% of this organic matter is mineralized, but what is left is no doubt in a condition very different from what it was previously: structural changes make it much more susceptible to the action of soil micro-organisms.

Wherever the earthworm community is less diversified than in Lamto, as in Sudanian savannas or in man-made tropical pastures, the mechanical action of the worms is less important. However, the few observations so far made at Foro Foro and Laguna Verde show that it is still far from negligible.

Soil mixing by earthworms changes its texture, which becomes fine grained in its upper layers, where their mechanical action is more important. The production of surface casts also prevents the packing down of the topsoil. The volume of material raised above soil surface (30–40 m³ ha⁻¹ yr⁻¹ at Lamto) corresponds to an equal amount of air below ground level. In the long run, the accumulation of casts can lead to a uniform layer of fine-grained soil.

Interactions between earthworms and microorganisms

Some laboratory experiments carried out on *Millsonia anomala* casts by Lavelle et al. (1980) point to a possible competition between worms and soil micro-organisms for the exploitation of the more easily digestible and energy-rich substrates. Such a competition would not be apparent when food is in excess, but would appear when conditions are less favourable. However, earthworms can also profit from micro-organisms when they feed upon degradation products of substances, such as cellulose or hemicellulose, which they cannot digest themselves.

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